SEXUAL DIMORPHISM AND REPRODUCTIVE BEHAVIOR IN *ALMYRACUMA PROXIMOCULI* (CRUSTACEA: CUMACEA): THE EFFECT OF HABITAT

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ABSTRACT

Individuals of *Almyracuma proximoculi* are the least sexually dimorphic cumaceans known, because the males are progenetic, *i.e.,* they are precociously sexually mature at a morphologically immature state. This species lives in dense aggregations in the upper intertidal zone and has eliminated the morphologically complex, apparently pheromone-sensitive, and highly motile terminal male stage found in other cumacean species. The sexually dimorphic characters that are present are predominantly ones that facilitate the rapid removal of the female's exuviae by the male during her fertilization molt. The removal rate is critical, because the partially detached exuviae blocks access to the female's ventrum. With the exception of the rudimentary penes found in two genera, male cumaceans do not possess an intromittent organ and apparently must deposit one or more spermatophores on the female's ventrum before the developing oostegites completely enclose this area.

INTRODUCTION

Cumaceans belong to the superorder Peracarida, which also includes amphipods, isopods, tanaidaceans, and mysidaceans, among others. The Cumacea are infaunal peracarid crustaceans that are primarily marine and are found world-wide from the intertidal zone to abyssal depths (Jones, 1976). Sexually immature males and females have very similar external morphologies and ornamentation, and most of the sexually dimorphic characters are acquired in the last few molts (Zimmer, 1941).

Like most Peracarida, cumaceans brood their young in a ventral marsupium, and the most striking change in female morphology is the rapid and complete development of the oostegites in only two molts. The external development of the male is typically a more gradual process and involves the sexually dimorphic development of a variety of body parts (Forsman, 1938; Granger *et al.,* 1979; Bishop, 1982). Commonly this differential development of the male includes, but is not limited to, the following: an increased number and greater development of natatory thoracic exopodites; the presence of up to five pairs of natatory pleopods which, with the exception of one species, are never present in females; a less spinose carapace that generally has a lower profile than that of the conspecific female; and the flattening and broadening of various appendages and projections such as the epimeral plates of the thoracic and abdominal somites. No one species possesses all of these adaptations in their most developed forms, but typically a male cumacean will exhibit a combination of several of them, as in *Diastylis cornuta* (Fig. 1).

In addition to the above changes, the greatest differential development occurs in the male's second antennae. The second antennae of mature male cumaceans
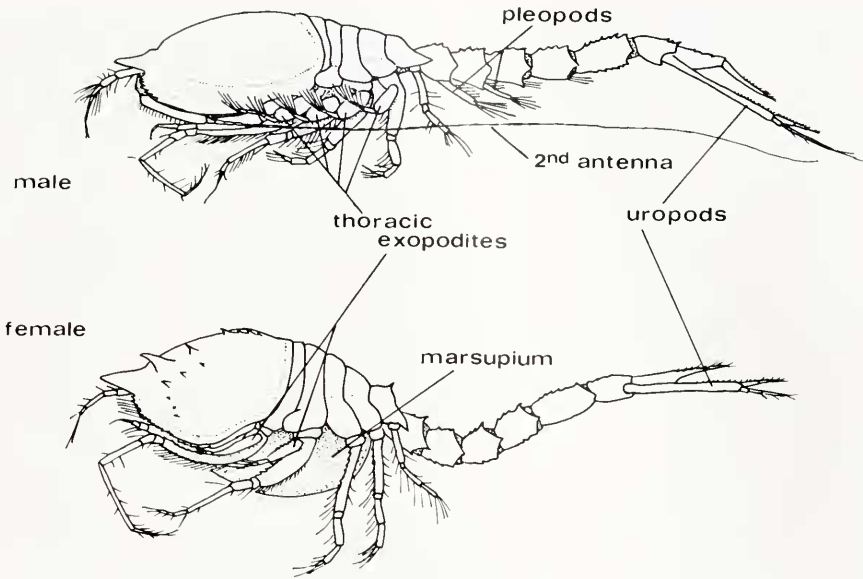
FIGURE 1. Copulatory male and marsupial female of *Diastylis cornuta* (after Sars, 1900).

are always well developed, with the exception of one species, while those of females are always rudimentary (Jones, 1963). In many species they equal or exceed the male's total body length (Sars, 1900). The development of these enormous antennae only in sexually mature male instars suggests that they are probably chemosensory, serving as the receptors for pheromones released by females before their fertilization molts, as has been demonstrated in the Amphipoda (Dahl *et al.,* 1970; Lyes, 1979). These two modes of differential development produce a motile, chemically sensitive male which is able to swim up into the water column and seek out potential mates.

The cumacean *Almyracuma proximoculi* Jones and Burbanck, 1959, is a small crustacean, with sexually mature individuals ranging from about 2.3 to 4.3 mm in length (Duncan, 1981). It has been collected in low numbers in estuarine areas from Currituck Sound, North Carolina, to Cape Cod, Massachusetts (Jones and Burbanck, 1959; Sanders *et al.,* 1965; Boesch and Diaz, 1974; Crandall, 1977; Ristich *et al.,* 1977; Menzie, 1980; T. E. Bowman, Smithsonian Institution, pers. comm.), but its optimal habitat appears to be thermally moderated areas in the immediate vicinity of freshwater springs in the upper intertidal zone of Long Island, New York, and southern New England. It inhabits these areas year-round, typical densities within a few meters of these groundwater discharges range from 3000–4500 m^{-2}, and extrapolated densities as high as 31,000 m^{-2} have been recorded in these areas (Duncan, 1981). This species is essentially restricted to these disjunct, intertidal aggregations with high within-habitat densities and proportionately large distances between aggregations.

MATERIALS AND METHODS

Random samples of ten preparatory females and ten copulatory males from an intertidal freshwater spring in West Falmouth Harbor, Massachusetts, were measured with an ocular micrometer (±0.0196 mm). All dimensions are from the left

sides of individuals, with the exception of the cross-sectional area of the fifth abdominal somite.

Laboratory observations were made on over 600 clasping pairs of individuals (copulatory male and preparatory or marsupial female). These individuals were collected from intertidal freshwater springs at the following localities on Cape Cod, Massachusetts: West Falmouth Harbor, Waquoit Bay, and Pocasset. Most of the individuals were maintained as isolated pairs in multicompartmented, transparent, plastic trays for up to four months. In addition to the animals, each compartment contained 20 ml of water and a small amount of sand from a collection site. Additional observations were made on groups of individuals maintained in glass finger bowls with varying amounts of water and substrate. Specimens for scanning electron microscopy were fixed in 5% glutaraldehyde for 10 min at room temperature, transferred to 95% ethanol, and air-dryed on double-sided adhesive tape.

<div align="center">RESULTS</div>

Morphology

The external morphology of the copulatory male of *A. proximoculi* is very simple (Fig. 2) and provides a sharp contrast to typical copulatory male cumaceans (Fig. 1). Neither sex has pleopods. Both sexes have a moderate and equivalent development of the thoracic exopodites, show similar profiles and smoothness of the carapace, and lack pronounced flattening and broadening of appendages or body parts. The male's second antenna is rudimentary and comparable to that of the female (Jones and Burbanck, 1959). With the exception of the developing oostegites of the female and the consequent greater width of her thorax, there are few other obvious morphological differences between the sexes.

The limited sexual dimorphism that is present in *A. proximoculi* is expressed mainly in the disproportionate development of the copulatory male's third maxillipeds and first pereiopods (Fig. 2) and of most of the post-thoracic region of his body (Fig. 2, Table I). On average, the abdomens of copulatory males are 31% longer and have a 55% greater cross-sectional area when compared to those of preparatory females of similar carapace lengths. Additionally, the uropodal peduncles of these males are 65% longer and 25% wider than those of the females (Table I; Fig. 3A, B). In contrast, the male uropodal endopods are only 7% longer than the female ones, equivalent to the average difference in carapace lengths between the two groups.

Although there are no other major differences between the sexes in the general shape, sculpturing, or ornamentation of the integument, the medial surfaces of the male's uropodal peduncles and endopods are armed with two distinct types of spines which are arranged in single rows. Those found on the endopods are simple, cone-shaped projections which are more numerous on the male than on the female (usually six *versus* two, Fig. 3A, B, D). The second type is a complex, pinnate form (Fig. 3C) which is absent on female or less mature male stages. There are usually six to ten of these on each uropodal peduncle of a copulatory male. The same margin of female and earlier male instars carries only a few simple setae (Fig. 3A). The other margins of the uropodal appendages of both sexes are either bare or carry simple setae only (Fig. 3A, B).

Behavior

In late winter, throughout the spring, and during summer mature males will clasp preparatory females. During precopula the female is clasped and manipulated

FIGURE 2. Scanning electron micrograph of a precopulatory clasping pair of *Almyracuma proximoculi*. The preparatory female is being held by the male's third maxillipeds and first pereiopods.

with the male's oversized third maxillipeds and first pereiopods (Fig. 2). She is usually carried in the same posterior-anterior alignment as the male with her dorsum adjacent to the male's ventral surface (2951 of 2962 observations). Unless disturbed, clasping pairs generally lie on their sides on the bottom of the observation dish, or if enough sediment is present, they remain buried. When disturbed they often swim up into the water, using the thoracic exopodites of the male and occasionally those of the female for locomotion. Males were never observed feeding while clasping females, but clasped females continue to feed normally by grasping sand grains and rotating them against their mouthparts. It is unknown how long pairs will remain in a clasped position in the field, but in laboratory conditions males have clasped

TABLE I

Mean dimensions and their standard errors of Almyracuma proximoculi

	Carapace length	Abdomen length	Cross-sectional area of fifth abdominal somite ($\times 10^3$)	Uropodal peduncle length	Uropodal peduncle width	Uropodal endopod length
preparatory female	851 ± 12.3	1494 ± 24.0	37.9 ± 1.01	282 ± 9.8	98 ± 1.4	255 ± 5.1
copulatory male	894 ± 15.8	1952 ± 30.4	58.9 ± 1.89	465 ± 8.8	123 ± 7.3	272 ± 3.5
increase in male	5.05%	30.7%	55.4%	64.9%	25.5%	6.67%

All dimensions are in micrometers, except for cross-sectional areas in square micrometers, and are from random samples of ten individuals of each sex.

females for as long as four months when the fertilization molt was experimentally delayed by lowering ambient temperatures.

Normally, the male's abdomen is straight or slightly flexed, but occasionally he flexes it enough to grasp the female's abdomen immediately behind the thorax with his uropods. The male then straightens his abdomen rapidly, raking the medial surfaces of his uropods along her abdomen. If copulatory males are present that are not already clasping females, they will approach a clasping pair and attempt to dislodge the male. During these events and while trying to hold onto the female in any way possible, either male uses his oversized abdomen and uropods in two ways. He attempts to force his uropods between the other male and the female and pry them apart and/or he grabs the other male's abdomen with his uropods and attempts to pull him off the female.

The fertilization molt is initiated by the splitting of the female's exuviae on the dorsal midline of the five exposed thoracic somites. Immediately after this the male moves his first pereiopods under the loose thoracic segments of the exuviae and forces his third maxillipeds under the posterior margin of the exuvial carapace. The carapace then comes off in one piece. The five exuvial thoracic segments remain attached ventrally to each other and to the exuvial carapace and abdomen. Consequently, the detached portions of the exuviae hang beneath the female. The male than arches his abdomen, grasps the female's abdomen immediately behind the thorax with his uropods, and rakes the entire length of her abdomen with their inner surfaces (Fig. 4). This vigorous raking, involving considerable effort by the male, continues until the exuviae is pulled completely free from her abdomen. The male immediately turns the female over, reverses her anterior-posterior position, and briefly clasps her with their ventral surfaces opposed. Shortly thereafter ova can be seen within the marsupium. Females with fully developed marsupia very seldom elicit a response from males; but as soon as the young are released, and females molt back into a preparatory instar ("interbrood" stage, *sensu* Duncan, in prep.), mature males will clasp them.

DISCUSSION

The rudimentary state of the copulatory male's second antennae in *A. proximoculi* is unique among the approximately 1000 known species of Cumacea (Jones and Burbanck, 1959). The copulatory males of this species are progenetic (Duncan,
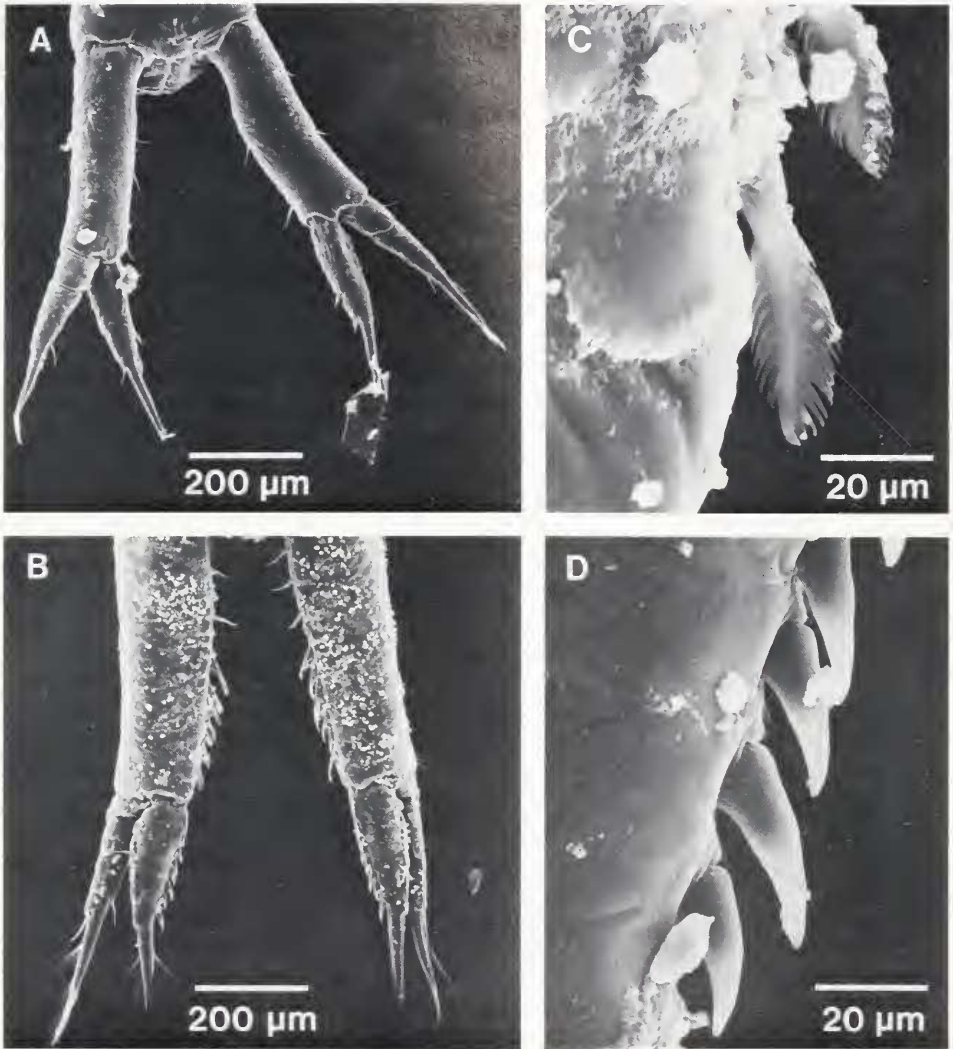
FIGURE 3. Scanning electron micrograph of the uropods of mature *Almyracuma proximoculi:* A) dorsal view of preparatory female; B) same view of copulatory male; C) dorsal view of two most distal spines on left peduncle in (B); D) dorsal view of middle spines on left endopod in (B).

1981), *i.e.,* they are precociously sexually mature at a morphologically immature state. I suggest that the typical distribution of this species in disjunct, dense, intertidal aggregations has eliminated the need for a pheromone-sensitive, highly motile, copulatory male. This distribution has apparently permitted this species to eliminate a morphologically complex instar that would normally be the final male stage and possibly reduces intraspecific competition for food resources that would otherwise be needed for the elaboration of body parts seen in the males of other species. In *Pseudocuma longicornis,* another cumacean species, "young males" clasp females, and "fully adult" males, although present, have never been observed in mating pairs (Foxon, 1936; Corey, 1969). This species is most common in low intertidal and
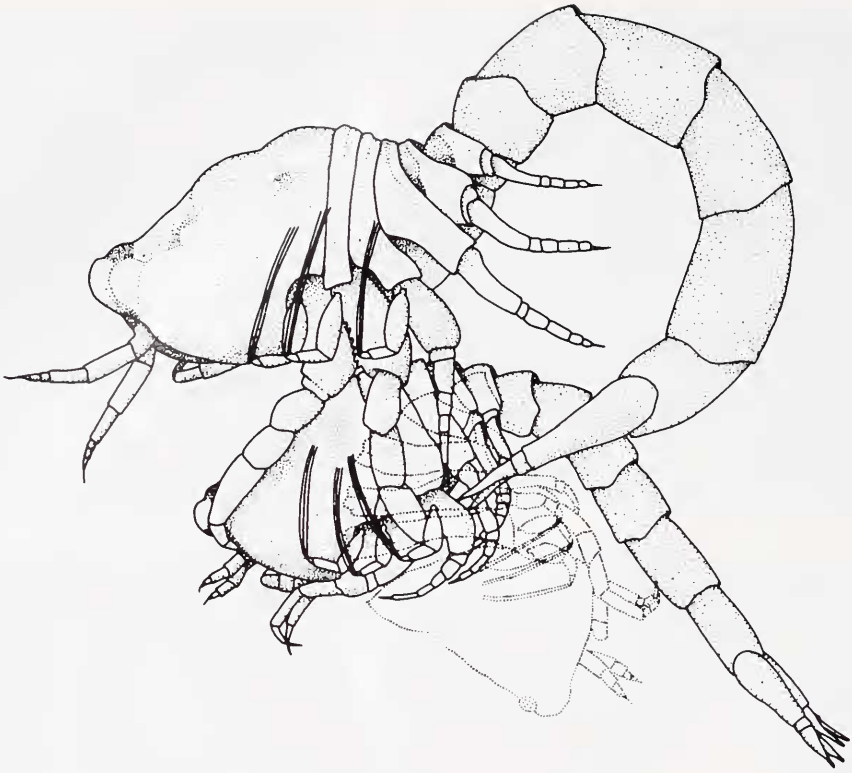
FIGURE 4. Precopulatory clasping pair of *Almyracuma proximoculi*, consisting of a copulatory male (top), a mature female (middle), and a partially detached exuviae (dotted outline at bottom).

shallow intertidal zones (Corey, 1970) and appears to be another example of progenetic development of copulatory males in a shallow water cumacean species.

The comparatively greater size and spination of the uropods of male cumaceans has been known for many years (Sars, 1900; Zimmer, 1941), and it has been suggested that these are adaptations for cleaning adhering material from the mouthparts and other appendages (Dixon, 1944). This function alone can not explain the striking sexual and ontogenetic differences seen in the uropods and abdomen of *A. proximoculi* and other species, since both sexes and the various instars of a particular species generally occur in the same substrate and can be expected to have the same cleaning requirements. Additionally, there is a distinct shift of morphological emphasis in the males of *A. proximoculi* from the enhancement of natatory functions to improving the males' ability to clasp and manipulate females.

The precopulatory clasping posture utilized by *A. proximoculi* (female dorsum clasped to male ventrum with both individuals in the same anterior-posterior alignment) is the same as has been noted in other Cumacea (Zimmer, 1941), with the exception of *Mancocuma stellifera* (Gnewuch and Croker, 1973) and *Spilocuma salomani* (Saloman, 1981). Saloman, citing Jones and Burbanck (1959), stated that male *A. proximoculi* grasp female abdomens with their second antennae. Apparently he misread the latter paper. The rudimentary development of these antennae (Jones and Burbanck, 1959; personal observation) makes such behavior impossible. Due to the position of the female's body and the use of the male's appendages for clasping, this posture probably precludes feeding by the males of most species during this period.

However, this may be unimportant, since the copulatory stage is usually a terminal one for male cumaceans, and most males die soon after mating. A similar nonfeeding pattern occurs in the copulatory males of several species of Tanaidacea, where the mouthparts are reduced and the anus is fused shut (Gardiner, 1975). Conversely, the elaborate natatory and sensory appendages seen in typical copulatory male cumaceans are maladaptive for the infaunal, burrowing lifestyle of young males and do not develop fully until the terminal instar.

Preparatory females and other developmental stages, including all of the immature male instars, molt successfully without aid in the laboratory. Therefore, it appears that the male's differential development and behavior serve only to accelerate the female's fertilization ecdysis. With the exception of the rudimentary penes found in two genera, *Archeocuma* (Băcescu, 1972) and *Campylaspenis* (Băcescu and Muradian, 1974), intromittent organs are unknown in the Cumacea, and sperm are extruded from two pores on the ventrum of the fifth thoracic somite. The partially detached exuviae blocks access to the female's thoracic ventrum, and shortly after molting the fully developed oostegites overlap each other considerably, completely enclosing this area. Thus the removal rate is critical, if the male is to gain access to this area and deposit a spermatophore successfully.

The unusual habitat of *A. proximoculi* has influenced both the morphology and the behavior of this species. High levels of chemosensitivity and swimming ability may not be particularly advantageous in a species, such as this one, that has a distributional pattern of high local densities in an intertidal area and relatively large distances between aggregations. Instead, the ability to rapidly remove a female's exuviae once molting has started and to deposit a spermatophore before the ventrum is enclosed by the marsupium or interruption and/or displacement by a competing male occurs appears to have influenced the morphology of the male of this species. *Almyracuma proximoculi* represents one end of the spectrum of morphological complexity and swimming ability found in male cumaceans that may be controlled, ultimately, by the densities of potential mates and competing males.

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